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Contemporary fire regimes in a fragmented and an unfragmented landscape: implications for vegetation structure and persistence of the fire-sensitive malleefowl

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Abstract. Habitat fragmentation alters fire regimes by changing the spatial and temporal context in which fire operates, potentially altering ecosystem state and threatening taxa. In the fragmented wheatbelt of Western Australia, spatial patterns of contemporary fire and their effects on biodiversity conservation are poorly understood. We addressed this by: (1) determining if fire regimes differed between vegetation remnants of differing sizes and uncleared vegetation, using analysis of satellite imagery; (2) determining vegetation structural responses to time since fire in three habitats: mallee-shrub, *Acacia* shrublands and mallee-heath; and (3) exploring the consequences of these differences, using the fire-sensitive malleefowl (*Leipoa ocellata*) as a case study. Fire was infrequent in small remnants, more frequent in large remnants, and most frequent in uncleared areas. Key vegetation structural attributes for malleefowl, such as canopy and litter cover, increased beyond 45 years post-fire in mallee-shrub, reached a plateau in mallee-heath after 30–40 years, and declined in *Acacia* shrublands after 25–40 years. Senescence in long-unburnt vegetation, combined with rare contemporary fires, suggest progressive decline in habitat quality of *Acacia* shrublands for malleefowl in the wheatbelt. In the adjacent, continuously vegetated landscapes, more frequent (and extensive) fires in structurally developing mallee-shrub communities are of concern for malleefowl conservation.

Additional keywords: bird, chronosequence, habitat, remote sensing, senescence.

Introduction

Loss, fragmentation and degradation of vegetation in agricultural landscapes have led to declines in biodiversity worldwide (Fahrig 2003; Hobbs and Yates 2003). Among the effects on species and communities, fragmentation can lead to secondary effects on ecological processes such as the fire regime, by altering the spatial and temporal context in which fire operates (Baker 1992; Ford *et al*. 2001). Consequently, fire often no longer operates as a natural disturbance regime in fragmented landscapes (Baker 1992; Hobbs and Yates 2003).

Fragmentation can have diverging effects on fire regimes in remnant vegetation depending on the social and environmental context in which the remnants are located (Gill and Williams 1996). Increases in fire frequency – one component of a fire regime – occur in some remnants as they are exposed to more intensive use by humans and greater sources and frequency of ignition (Kemper *et al*. 1999; Tabarelli and Gascon 2005). In other cases, the displacement of traditional human societies and their active fire management practices, discontinuous vegetation cover and advances in fire suppression may lead to declines in fire frequency in remnants (Hobbs and Yates 2003; McCaw and Hanstrum 2003).

Changes in the fire regime can lead to altered ecosystem state and constitute a threatening process for many taxa (Garnett and Crowley 2000; Burgman *et al*. 2007). At the community scale, the fire regime can be the predominant force driving community assembly (Verdú and Pausas 2007) and successional processes (Noble and Slatyer 1980). Disturbances from fire initiate vegetation redevelopment (Hobbs 2003), although the community that exists following fire may be somewhat idiosyncratic depending on the nature of the fire, the pre-existing community, the accumulated fire history and post-fire factors (Noble and Slatyer 1980; Bond and van Wilgen 1996). This process is of considerable theoretical and management relevance.

From a theoretical perspective, changes over time allow exploration of the role of fire in regulating vegetation composition and structure, relative to the role of climate (Bond *et al*. 2005). In the long-term absence of fire, does vegetation in fire-prone ecosystems change little in composition or structure,

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being limited by climate or non-fire factors? Alternatively, does it continue to develop in stature long beyond the average inter-fire interval, being limited by climate but modified by fire? Or are fire-prone communities replaced by different communities, or do components of the community decline and senesce (the current community being fire-maintained) (Horton and Kraebel 1955; Hopkins and Robinson 1981; Bond *et al.* 2005)? From a biodiversity management perspective, patterns of vegetation change with time since fire could provide a useful indicator as to when fire management interventions may be necessary, such as to prevent undesired vegetation community change (Lunt 1998).

Structural parameters are fundamental in determining the suitability of vegetation as habitat for many animals (MacArthur and MacArthur 1961; Clarke 2008). The malleefowl (*Leipoa ocellata* Gould) is a large (~2 kg), sedentary, ground-dwelling bird that is listed as vulnerable (IUCN 2008). This species occurs in mallee-shrub and semiarid shrublands across southern Australia, habitats that are considered highly prone to fire (Noble *et al.* 1980; Hodgkinson 2002). Consequently, malleefowl persistence is inextricably linked to fire, with inappropriate fire regimes among the primary threats to its existence (Garnett and Crowley 2000; Benshemesh 2007). Fire incidence in agricultural landscapes in southern Australia is thought to have decreased compared with that in unfragmented landscapes (Gill and Williams 1996), although no studies have demonstrated this empirically. Large-scale wildfires, however, have a severe and long-lasting effect on malleefowl populations (Priddel 1989; Benshemesh 1990).

Malleefowl prefer long-unburnt habitat (at least 40 to 60 years), as it possesses key vegetation structural attributes. A near-continuous canopy provides shelter from predators and weather, whereas plentiful leaf litter is important for nest mound construction and harbouring food (Benshemesh 1992). In addition, a diverse and abundant shrub understorey provides an important food resource (Harlen and Priddel 1996). How might these habitat elements be affected by time since fire? In the absence of fire for periods well in excess of that typical for a community (e.g. >46 and >66 years for shrublands and mallee-shrub respectively; O'Donnell *et al.* 2011), communities that are limited by climate but modified by fire could be predicted to have increased woody cover (Bond *et al.* 2005), including increasing canopy cover and height and increased leaf litter, suggesting increasing habitat suitability for malleefowl with time. Alternatively, if communities are regulated by climate, woody vegetation parameters could be expected to plateau within a typical fire cycle, indicating a maximum and stable suitability for malleefowl beyond a specific age post-fire. In fire-maintained communities, a decrease in woody vegetation parameters would be expected in the oldest vegetation, indicating a peak period of malleefowl habitat suitability at an intermediate age post-fire.

In this study, we aimed to determine the effect of fragmentation on the fire regime, the ecological implications of differences in the fire regime on vegetation structural development in three major habitats in the Western Australia (WA) wheatbelt (mallee-shrub, *Acacia* shrublands and mallee-heath), and, using the habitat requirements of the malleefowl as a case study, explore the biodiversity conservation consequences of any fire regime differences.

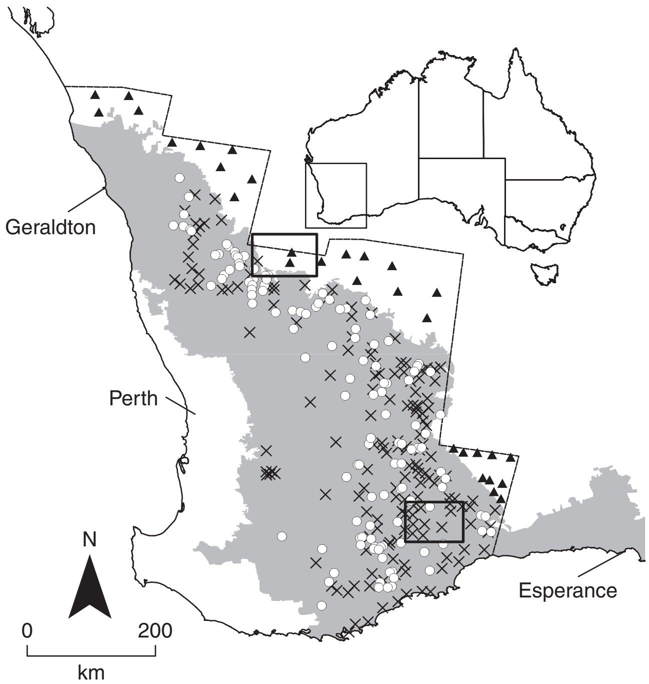

Fig. 1. Study area. Shaded area illustrates Western Australian wheatbelt, white circles represent small remnant samples, crosses represent large remnant samples, triangles represent continuous vegetation samples; bold rectangles represent study areas for habitat analysis (*Acacia* shrubland was sampled in the north, and mallee-shrub and mallee-heath in the south); thin solid line represents limits of imagery used in analysis.

Methods

Contemporary fire regimes in and adjacent to the WA wheatbelt

Study area

We analysed contemporary fire regimes in the WA wheatbelt (31.5°S, 117.5°E) and uncleared areas up to 100 km to the east (Fig. 1). Since European colonisation, over 93% of the native vegetation in the WA wheatbelt has been removed, largely for cereal cropping and sheep grazing (Saunders *et al.* 1993). The intensity of land use has led to its ranking as one of the most stressed landscapes in Australia (National Land and Water Resources Audit 2001).

The uncleared lands on the eastern edge of the wheatbelt are relatively undisturbed, containing vast tracts of intact vegetation communities similar to those of the wheatbelt (e.g. shrublands, heaths, woodlands and mallee-shrub; National Land and Water Resources Audit 2001). Land uses are primarily extensive pastoralism, mining, nature conservation and vacant crown land. This provides an opportunity to compare fire regimes of these ecologically similar landscapes that now differ in social and environmental context.

Analysis of satellite imagery

To quantify the spatial extent and frequency of fire, we made use of a temporal sequence of satellite images (Landsat Thematic Mapper, calibrated as part of the LandMonitor project; Caccetta *et al.* 2000) consisting of summer images for every

2 years between 1988 and 2004 (for technical details, see Caccetta *et al*. 2000). For each time step within the sequence, we identified fire events by determining areas showing clear increases in reflectance between successive images. A 100-m cell resolution was used in a supervised classification in a Geographic Information System (Spatial Analyst, *Arcview 9.1*). Burns in the 5 years preceding 1988 were identified by a conspicuous decrease in reflectance (i.e. vegetation recovery) between satellite images for the first time step in the sequence, 1988 to 1990. Some visual interpretation was required to distinguish between burnt cells and other types of change such as vegetation clearing or intermittent waterbodies.

We compared the frequency and spatial extent of fire events between 1988 and 2004, and for the 5 years preceding 1988, for three groups of samples within the study area: small remnants (100 to 500 ha); large remnants (>500 ha); and continuous vegetation adjacent to the wheatbelt in the extensive land-use zone (Fig. 1). Samples for the small and large remnant groups were selected based on the following rules: (1) malleefowl had been sighted within 1 km of the remnant after 1988 (see Parsons *et al*. 2009 for a detailed description of this dataset); and (2) remnant was not contiguous with the extensive land-use zone. Although this sampling regime was designed for another study, we believe it is representative of remaining vegetation in the wheatbelt (as woodlands, which were not specifically sampled, were disproportionally cleared; Burvill 1979). If woodlands were under-represented in the wheatbelt sample compared with the uncleared landscape, it would likely lead to the underestimation of wheatbelt fire incidence, as woodlands burn less frequently than shrublands or mallee-shrub (O'Donnell *et al*. 2011). All samples excluded non-flammable saltland vegetation.

For small remnants, the entire remnant was examined for evidence of fire. For large remnants, we examined one randomly placed, circular 500-ha sample in remnants 500 to 10 000 ha, and five randomly placed 500-ha circular samples in remnants >10 000 ha. For remnants where the circular sample did not fit completely within the remnant (e.g. linear remnants), the 500 ha nearest the sample centroid was used. For continuous vegetation adjacent to the wheatbelt, 500-ha circular samples were placed at random within 100 km of the boundary with the wheatbelt and within the bounds of the imagery. The following measures were summarised for each of three landscape context groups (small and large remnants and continuous vegetation):

- Evidence of recent fire before 1988;
- Number of fire events that occurred between 1988 and 2004;
- The cumulative proportion of the sample burnt between 1988 and 2004.

Vegetation structural development after fire

Study areas

We examined how vegetation recovered from fire by conducting a space-for-time study within two areas in south-west WA. The two areas were selected because they contained a range of fire-age classes within three fire-prone broad vegetation structural classifications: mallee-shrub, mallee-heath and *Acacia* shrublands. One area based around Lake Magenta and Dunn Rock Nature Reserves in the south-eastern wheatbelt (Fig. 1) supported closed mallee-shrub (e.g. *Eucalyptus phaenophylla* Brooker and Hopper and *E. scyphocalyx* (Benth.) Maiden & Blakely) communities with understoreys of various *Melaleuca* shrubs interspersed with proteaceous mallee-heath. Mallees are multistemmed *Eucalyptus* spp. that sprout from underground lignotubers after disturbances. They form the dominant tall vegetation stratum in mallee-shrub communities, and occur as scattered emergents in mallee-heath. The second area was situated at Charles Darwin Reserve and Mount Gibson Sanctuary, adjacent to the northern wheatbelt (Fig. 1). The vegetation consisted largely of mixed shrublands (*Acacia coolgardiensis* Maiden, *A. stereophylla* Meisn., *Allocasuarina acutivalvis* (F.Muell.) L. A. S. Johnson, *A. campestris* (Diels) L. A. S. Johnson, *Melaleuca* spp.) interspersed with open woodlands (Beard 1990).

Site selection

We used fire history mapping (Department of Environment and Conservation, unpubl. data 2006) to summarise fire regimes and delineate various fire ages within each study area. Five transects were placed in each fire age within each vegetation community except where noted. In mallee-shrub and mallee-heath, we sampled the following fire-age classes: 3–4, 6, 18–20, 25, 30, 35, 39 and >45 years (mallee-heath >45 years contained eight transects). In *Acacia* shrubland we sampled 5, 7, 12, 15, 22 (three transects), 27 (three transects), 30 (three transects), 38 and >45 (six transects) years. The exact year of fire for areas burnt before 1968–69 was not known and so was set at the minimum possible year, 1962 (i.e. 45 years or more post-fire), for the purposes of analysis.

With space-for-time studies, random error and pseudoreplication are important issues as (1) it may be difficult to locate sample sites that are truly comparable with one another (Oksanen 2001); and (2) replicates may fall within one instance of a treatment and so may not be truly independent (e.g. sample sites within the one fire scar) (Hurlbert 1984). To minimise such bias within the present study, transects were located in separate fire scars within the same fire-age class where possible, or if not, at least 150 m apart. In addition, transects were limited to locations with comparable vegetation species composition. In mallee-shrub, 13 individual fire events were sampled across seven vegetation ages (range of one to three fires per age, with an unknown number of fires affecting sites last burnt pre-1968). In *Acacia* shrubland, nine individual fire events were sampled across nine vegetation ages (i.e. one fire per age, with an unknown number pre-1968). In mallee-heath, 13 individual fire events were sampled across seven vegetation ages (range of one to two fires per age, with an unknown number pre-1968). Data on factors such as season of burn, long-term fire history, fire intensity and post-fire conditions were not available and so could not be incorporated into the study.

Field measurements

Transects 100 m long were placed within each replicate of vegetation × fire-age combination. At each transect, a 4-m pole was placed at 2-m intervals (50 per transect) recording the presence or absence of live vegetation intercepting the pole in each height interval (0–12, 12–25, 25–50 cm, 50 cm–1 m; 1–2, 2–4, >4 m) (Benshemesh 1992). Litter cover was quantified by making point observations 1 m to either side of the 50 pole placements (i.e. total of 100 litter measurements) with observations falling into one of four categories: (1) litter >1-cm depth, (2) litter <1-cm depth, (3) bare ground, (4) shrub or herb (i.e. obstructed by low shrubs or ground cover). Field measurements were designed to quantify important changes in vegetation structure, and specifically those considered important to malleefowl (i.e. canopy, understorey shrubs and litter cover), with respect to time since fire. Mallee-shrub and *Acacia* shrubland measurements were taken during winter (June to August) 2007, and mallee-heath in autumn and winter 2008.

Statistical analysis

We calculated the average fire interval for each of the three landscape context groups by an extrapolation based on the probability of any sample being burnt within the 16-year time period (1988 to 2004). Additionally, the calculation was performed for a 21-year time period (i.e. 1983 to 2004) incorporating fire events detected before 1988 to provide an indication of the sensitivity of the approach to temporal variation. The equation for calculating the average fire interval for each group is:

$$\text{average fire interval (in years)} = \frac{1}{(x/(y \times n))/z}$$

where x is the number of fire events within the time period; y is the number of observations within the time period; z is the number of years covered by each observation (in this study $z = 2$); and n is the number of samples. A worked example is given below using the ‘small remnant’ group:

- Eight observations $(y) \times 127$ remnants $(n) = 1016$ fire opportunities
- We observed six fires (x) in 1016 opportunities $\therefore$ $6/1016 = 5.905 \times 10^{-3}$ probability of a fire in any remnant in a 2-year period
- $5.905 \times 10^{-3}/2 = 2.9527 \times 10^{-3}$ = probability of a fire in a remnant in any 1-year period
- Interval for which a probability of a remnant burning = $1/2.9527 \times 10^{-3} = 339$ years.

The data measured fires at 2-year intervals, so multiple fires that occurred in the same sample within each 2-year period were treated as one. The calculation also assumed that each sample had an equal chance of being burnt. This estimate of fire frequency does not allow for decadal-scale climate variation (Cullen and Grierson 2009) and is estimated from a relatively short time-window.

Differences in the number of fires occurring between the three landscape context groups for both pre-1988–2004 and 1988–2004 were tested using Pearson’s chi square test.

For each vegetation height class and litter cover (>1 cm in depth) in each of the three habitats, we tested a set of regression models that represented four ecologically plausible outcomes for vegetation change (the number of intercepts per transect) with time since fire: an increase or decrease over time (linear, exponential); increasing but reaching a stable maximum

Table 1. Fire regimes for three landscape contexts within or adjacent to the Western Australian wheatbelt

Size class	Sample size	Percentage burnt 1988–2004 (number)	Percentage burnt pre-1988 (number)	Mean proportion of sample burnt (range)	Percentage of sites burnt more than once (1988–2004) (number)	Estimated fire interval 1988–2004 in years (95% CI)	Estimated fire interval 1983–2004 in years (95% CI)
100 to 500 ha	127	4.7 (6)	7.1 (9)	0.26 (0.01–0.53)	0 (0)	339 (156–909)	178 (108–317)
>500 ha	156	16 (25)	23 (36)	0.48 (0.01–1.0)	5.8 (9)	67 (49–96)	45 (36–57)
Unfragmented	30	33 (10)	40 (12)	0.69 (0.04–1.0)	3.3 (1)	40 (23–77)	26 (17–40)

Table 2. Summary of regression models for vegetation and litter cover versus time since fire for mallee-shrub, *Acacia* shrubland and mallee-heath
See Accessory publication for alternative models for each vegetation class

Class (cm)	Model form	Model	Percentage deviance explained	Standard error	P
Mallee-shrub					
400+	Logistic	$y = 0.23 + 15.75/(1 + e^{-0.972(x-32.37)})$	65.5	5.27	<0.001
200–400	Quadratic	$y = -7.32 + 1.847x - 0.0262x^2$	78.3	5.21	<0.001
100–200	Cubic	$y = -2.22 + 2.63x - 0.1158x^2 + 0.0015x^3$	31	5.56	<0.001
50–100		No significant relationship			
25–50		No significant relationship			
12–25	Negative linear	$y = 25.72 - 0.2094x$	18.0	6.03	0.004
0–12	Negative linear	$y = 33.83 - 0.4272x$	45.4	6.56	<0.001
Litter >1	Logistic	$y = 0.2179 + 36.57/(1 + e^{-0.2252(x-15.27)})$	73.8	8.14	<0.001
Acacia shrubland					
400+	Exponential	$y = 0.42 + 0.00022(1.28^x)$	41.3	6.02	<0.001
200–400	Logistic	$y = 0.1697 + 31.18/(1 + e^{-0.3471(x-25.54)})$	90.3	4.52	<0.001
100–200	Quadratic	$y = -6.6 + 2.757x - 0.05205x^2$	49.6	8.11	<0.001
50–100	Cubic	$y = 3.68 + 3.39x - 0.1539x^2 + 0.001819x^3$	38.1	7.18	<0.001
25–50	Asymptotic	$y = 2.79 + 21.76(0.965^x)$	51.1	4.77	<0.001
12–25	Negative linear	$y = 17.18 - 0.305x$	38.4	5.43	<0.001
0–12	Negative linear	$y = 12.53 - 0.1931x$	23.6	4.79	<0.001
Litter >1	Cubic	$y = 7.32 - 1.49x + 0.1582x^2 - 0.002762x^3$	52.2	9.37	<0.001
Mallee-heath					
400+		No significant relationship			
200–400	Quadratic	$y = -1.792 + 0.355x - 0.00575x^2$	23.4	2.51	0.002
100–200	Positive linear	$y = 1.944 + 0.1466x$	21.0	3.96	0.001
50–100	Cubic	$y = 8.10 - 0.859x + 0.0881x^2 - 0.001397x^3$	65.4	5.43	<0.001
25–50	Cubic	$y = 17.78 - 0.761x + 0.0832x^2 - 0.001392x^3$	60.2	5.13	<0.001
12–25		No significant relationship			
0–12		No significant relationship			
Litter >1	Quadratic	$y = 4.91 + 0.96x - 0.009x^2$	35	9.97	<0.001

(asymptotic, logistic); an increase followed by a decrease (i.e. senescence; quadratic), and fluctuation over time (e.g. the growth of successive vegetation layers through the height class over time; cubic). This fourth model was not relevant for the uppermost height class and was therefore not tested. The most parsimonious model for each parameter was selected using Akaike's Information Criterion (AIC), using GENSTAT Tenth Edition (Lawes Agricultural Trust), and is presented here. Where AIC was equal, the model with the greatest deviance explained was selected. All other models are included in the Accessory publication (available from the journal online), so readers can evaluate alternative outcomes.

Results

Contemporary fire regimes in and adjoining the WA wheatbelt

Fire events were distributed non-randomly across the three landscape context groups, for both pre-1988 ($\chi^2_2 = 13.909$, $P < 0.001$) and 1988 to 2004 ($\chi^2_2 = 24.44$, $P < 0.001$). A higher than expected number of fires occurred in both the 'large remnant' and 'continuous' groups, with a lower than expected number in the 'small remnant' group.

Of the 127 small remnants sampled, only six (4.7%) were burnt in the period 1988 to 2004 (Table 1), and none were burnt more than once during that time. In larger remnants, 25 of 156 samples (16%) were burnt and of those, nine experienced multiple fires (up to four). In continuous vegetation, 10 (33%) samples experienced a fire between 1988 and 2004, with one sample burnt more than once during this time period (three times).

The fire events observed in samples in large remnants and continuous vegetation were often part of much larger fires (mean area = 26 900 ha, range = 7–393 000 ha) and burnt through a higher proportion of the sample area (Table 1). In contrast, fires in small remnants were all minor fires (mean area = 80 ha, range = 10–264 ha) and tended to burn through a lower proportion of the sample area.

Based on the frequency of fire for 1988 to 2004, the average fire interval for small remnants in the WA wheatbelt was ~339 years (Table 1). The average intervals in large remnants and continuous vegetation were 67 and 40 years respectively (Table 1). The trends described above remained when incorporating data from pre-1988 (Table 1); however, estimates of fire intervals decreased.

Development of vegetation structure post-fire

Development and maintenance of vegetation structure after fire differed between mallee-shrub, mallee-heath and *Acacia* shrublands (Table 2, Figs 2, 3), suggesting contrasting ecological implications of particular fire-return intervals. Mallee-shrub vegetation retained substantial cover in all height

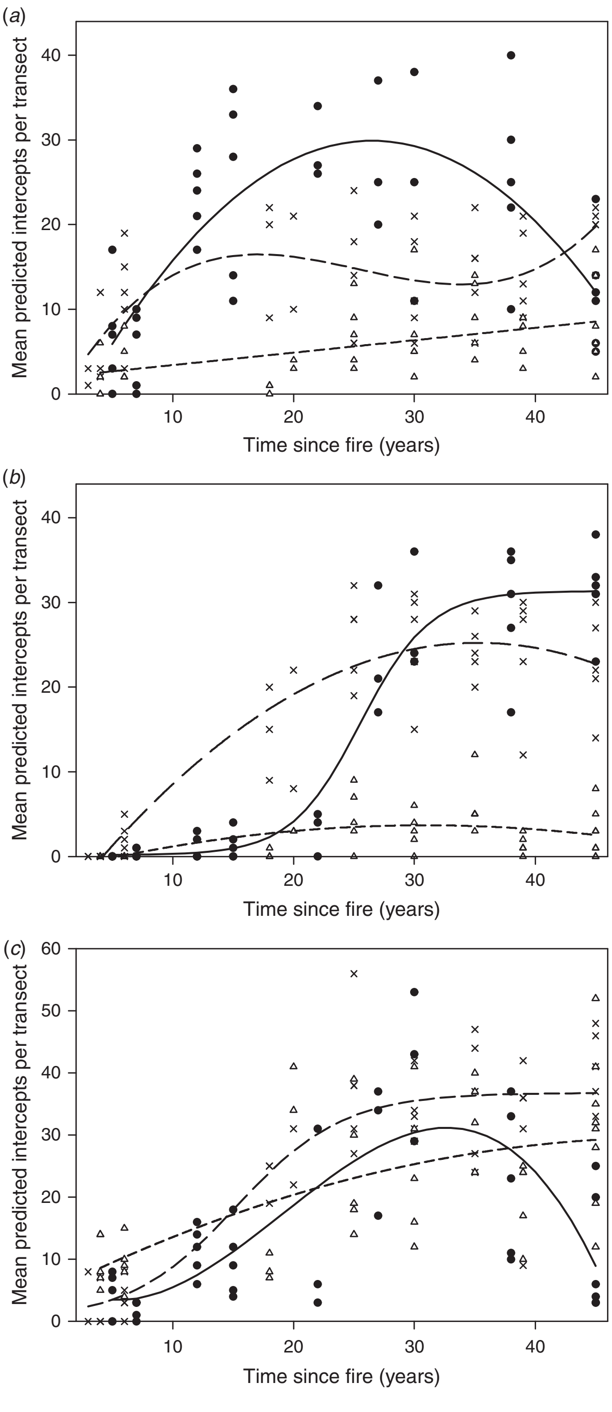

Fig. 2. Regression models describing the relationship between vegetation cover and time since fire for (*a*) vegetation 1 to 2 m; (*b*) vegetation 2 to 4 m; and (*c*) litter cover (>1-cm depth). Cross symbols and long-dashed line represent mallee-shrub; filled circles and solid line represent *Acacia* shrubland; open triangles and short-dashed line represent mallee-heath. See Table 2 for fitted model details.

categories over time, except for an absence of vegetation in taller height classes (>1 m) shortly after fire (<10 years) (Fig. 3). Vegetation <25 cm tall in mallee-shrub decreased over time from an initial peak within the first 10 years post-fire, but there was little change in vegetation between 25 and 100 cm. Vegetation between 1 and 2 m increased over time (Fig. 2*a*), indicating that a 1- to 2-m shrub layer established after ~10 years and remained until the >45 year limit of the dataset. Mallee-shrub vegetation developed a substantial canopy (2- to 4-m height class) after 20–25 years, with this canopy remaining intact for >45 years (Fig. 2*b*). The slight downward trend in mallee-shrub cover at 2 to 4 m beyond 30 years post-fire was due to the movement of cover through to the higher height class (>4 m, Fig. 3). Mallee-shrub deep litter cover (>1 cm) increased until ~25 years post-fire, where it then appeared to asymptote through to the limit of the >45 year dataset (Fig. 2*c*).

Acacia shrubland contained one dense vertical band of vegetation that increased in height over time (sometimes overlapping two height categories) with little vegetation cover remaining beneath it. The 1- to 2-m shrub layer in *Acacia* shrubland had high cover from 15 to 40 years post-fire, but declined considerably thereafter. The 50–100-cm category showed a similar pattern, but peaked ~10 years earlier. Development of upper vegetation layers in *Acacia* shrubland lagged that of mallee-shrub, with establishment of the 2- to 4-m layer occurring primarily 25–30 years post-fire, and the >4-m height class after >45 years. The accumulation of litter in *Acacia* shrubland was similar to that of mallee-shrub habitat until ~30 years post-fire, but after this time, litter decreased considerably, a trend not evident in the other two habitats.

Mallee-heath retained dense vegetation in all height categories <1 m over time, but owing to the lower stature and abundance of emergent mallees, there was little vegetation taller than 2 m at any time. Mallee-heath was alone among the habitats in having no decrease in vegetation <25 cm with increasing time post-fire. Cover of shrubs (50–200 cm) increased over time in mallee-heath, although the relationship between time since fire and vegetation cover at 1 to 2 m was weak. Litter cover in mallee-heath showed an asymptotic pattern similar to mallee-shrub, although it reached an asymptote at a lower litter cover.

Discussion

Contemporary fire regimes in and adjoining the WA wheatbelt

Analysis of satellite imagery indicated that the frequency of fire in and adjacent to the WA wheatbelt declined with increasing fragmentation. Fires were most frequent in continuous vegetation, least frequent in small remnants, with large remnants intermediate. Recent research indicates that in the continuously vegetated landscape adjoining the wheatbelt, long-term fire return intervals in shrublands and mallee-shrub were 46 and 66 years respectively (O'Donnell *et al*. 2011). Our results closely approximate these fire return interval estimates in the landscape contexts of continuous vegetation and large remnants over the period 1988–2004, albeit at the lower end in continuous vegetation. In contrast, there is strong evidence that the incidence of fire has declined substantially since fragmentation in small remnants, under the reasonable assumption that this region historically experienced an equivalent fire regime to that of adjoining, similar, continuously vegetated landscapes. In the heavily cleared landscape of the wheatbelt, fire appears to no

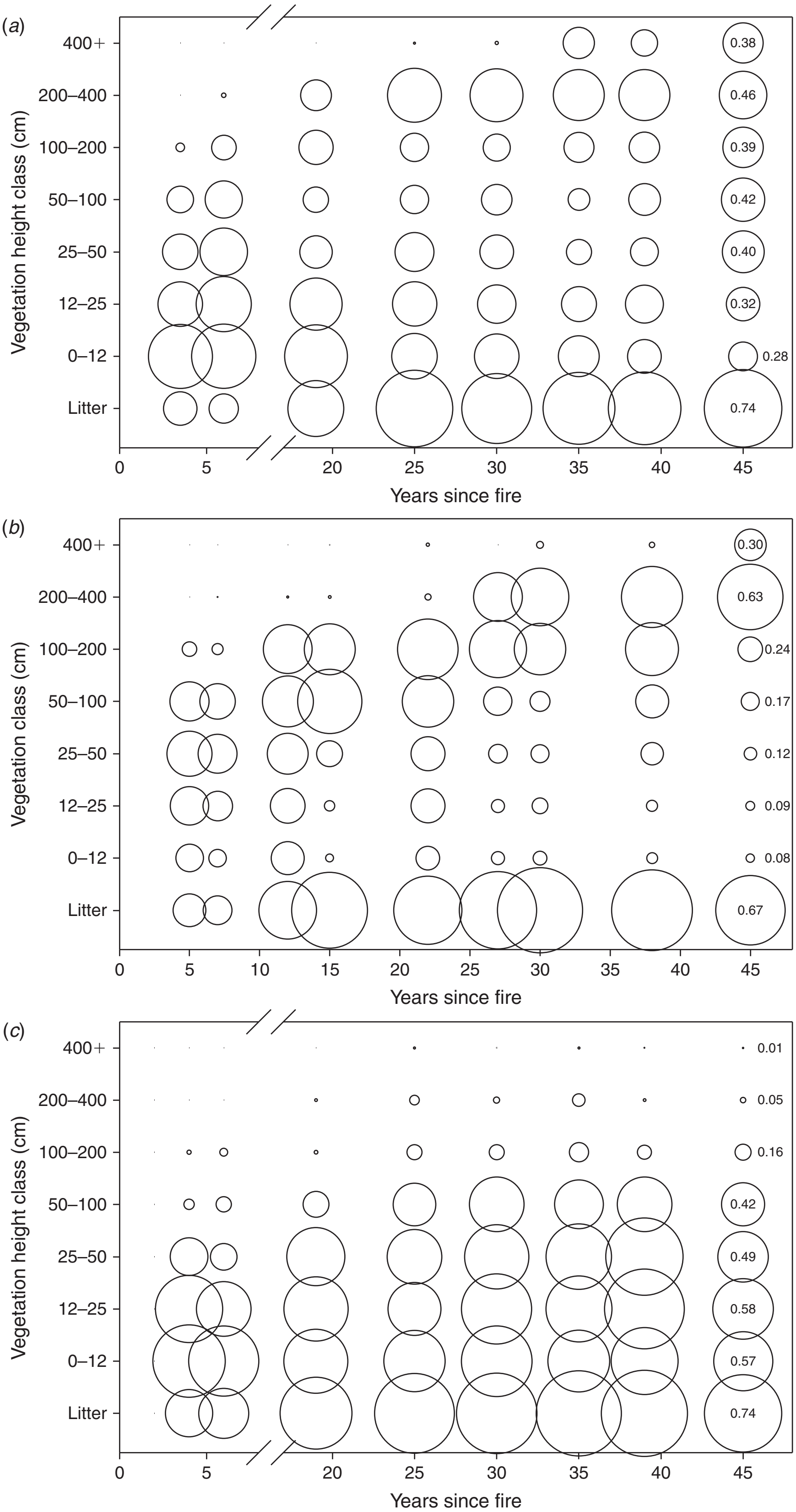

Fig. 3. Vertical vegetation profile and litter cover development with increasing time since fire for: (*a*) mallee-shrub; (*b*) *Acacia* shrubland; and (*c*) mallee-heath. Proportional cover is shown for litter and all vegetation height class bubbles for the 'unburnt' (i.e. >45 years) treatment for scale.

longer operate as a natural and functional disturbance (Baker 1992; McCaw and Hanstrum 2003).

There are several factors that may contribute to the relative infrequency of fires in small remnants. First, the agricultural matrix reduces the carriage of fires between remnants, as it has lower fuel loads over summer and provides opportunities for land managers to access and suppress fires (McCaw and Hanstrum 2003). Second, a lower proportion of native vegetation across the landscape reduces the likelihood of lightning ignitions in remnants. Third, total fire exclusion and fire suppression in native vegetation are widespread practices in farming landscapes because of the potential harm of fire to people and infrastructure. Despite this, the majority of fires that have affected wheatbelt remnants originate in non-natural ignitions in the agricultural matrix (Burrows *et al*. 1987), suggesting the infrequency of natural ignitions and the important role of vegetation connectivity in facilitating fire spread.

Interestingly, we showed that fires in small remnants tended to burn only a small proportion of the remnant (Table 1). This is in contrast to the view held by several authors (Priddel 1990; Hobbs 2003) that small remnants, although infrequently burnt, were more likely to burn in their entirety. Remnants and therefore fires are more accessible in fragmented landscapes and fires can often be effectively suppressed soon after establishment (McCaw and Hanstrum 2003), although large fires have occurred in agricultural landscapes elsewhere in Australia recently. In large remnants and remote areas adjacent to the wheatbelt, large, widespread fires were typical. These fires can burn unattended for weeks or months and exceed 100 000 ha (McCaw and Hanstrum 2003), owing to difficulties with access, low population densities, and lack of infrastructure necessitating a suppression response.

Fire interval estimates incorporating data from pre-1988 showed the same pattern between landscape contexts, but the intervals were substantially less than those for 1988 to 2004 only, suggesting that the incidence of fire was more common before 1988. Alternatively, the sampling method used to detect fires before 1988 may have sampled fires from a longer period than expected, resulting in an underestimation of fire return intervals.

For both sampling periods, the fire-return estimates were based on data spanning a short time period, which was less than the estimated intervals for all three landscapes. Multidecadal climate fluctuations (Cullen and Grierson 2009) and post-clearing changes in cloud formation process (Lyons 2002; which could lead to altered rainfall patterns) influence vegetation growth and could have a bearing on fire regimes (S. Prober *et al*., unpubl. data). The two different estimates of fire interval demonstrate the vulnerability of the method to sampling effort and climate fluctuations and should be considered as approximations.

It is plausible that landscape context groups differ in other attributes that affect their probability of burning. These may include climatic gradients and weather patterns (Lyons 2002), the vegetation type present (hence spatial distribution of fuel) relative to the probability of clearing (Burvill 1979), exposure to anthropogenic ignition sources (e.g. population centres, transport routes), human population density (Syphard *et al*. 2009), adjacent land use, remnant configuration and underlying biophysical properties (e.g. soils, topography). The paucity of fire instances in small and large remnants prevented us from taking a more predictive approach, so we have had to assume our landscape context samples are randomly distributed relative to these attributes. A more detailed analysis incorporating these factors into predictive models might be informative, and may become feasible as fire scar imagery continues to be collected, increasing sample sizes. Further, as the time spanned by these data increases, more accurate estimates of fire interval may be determined.

In addition to interpreting the current gross differences in fire return intervals between landscape contexts with reference to historic precedents, current regimes can also be considered in light of their effects on aspects of ecological condition, such as vegetation structure, and on species conservation, such as for the malleefowl.

Development of vegetation structure post-fire

The post-fire structural response of three habitats common in the WA wheatbelt differed, suggesting that fire may play a contrasting role in maintaining vegetation structure in each, despite the occurrence of these communities in a mosaic across the landscape.

Acacia shrubland showed evidence of being a fire-maintained community, as litter and some vegetation cover classes decreased 25 to 40 years post-fire, indicating a decrease in productivity and senescence in the long-term absence of fire (Gardner 1957; Yates and Broadhurst 2002). To maximise understorey and litter complexity in *Acacia* shrublands, and thus habitat suitability for malleefowl, fire intervals could be in the order of 25 to 40 years. Other intervals, however, might be appropriate for other fauna (Burrows and Abbott 2003; e.g. longer intervals for hollow-dependent species) or other objectives. In the WA wheatbelt, a continuation of contemporary fire frequencies may result in diminishing understorey and litter layer complexity; thus, it may be appropriate to promote fire in small remnants of this habitat to stimulate recruitment and rejuvenation of senescent vegetation and increase habitat suitability for malleefowl.

Of the habitats and locations sampled, mallee-shrub appeared to exhibit the most sustained productivity, as evidenced by the rate and trajectory of increase in litter and vegetation cover and height over time. Mallee-shrub continues to develop in stature in the long-term absence of fire, although fire may have a role in maintaining the mallee-shrub structural formation at fire-return intervals greater than those able to be examined in this study, as suggested by Hopkins and Robinson (1981). However, a continuation of contemporary fire regimes in small fragments is likely to result in less community degradation than in *Acacia* shrublands, at least in the short to medium term. In mallee-shrub habitat, fire intervals in excess of 45 years over substantial parts of the landscape would allow for ongoing vertical development while maintaining maximal understorey and ground layer complexity. These habitat elements are of known importance to several species of conservation concern occurring in the wheatbelt and adjoining regions, including malleefowl (Benshemesh 2007; Priddel *et al*. 2007).

In contrast to the other habitats (in which vertical extension continued through to the oldest age class), mallee-heath appeared to reach its maximum vertical potential ~30 years post-fire, by which time vegetation cover in all height classes appeared to plateau, suggesting that growth and productivity had peaked. This is a similar pattern to that reported by McCaw (1997) for the higher-rainfall Stirling Range, although the length of time until growth reached a plateau was greater. We are unable to determine from the present study whether this state would be maintained over time or if senescence would commence, but Maher (2007) indicates that community change to *Allocasuarina*-dominated woodland can occur in some locations in the long-term absence of fire, suggesting that the mallee-heath community is fire-maintained. The absence of change in vegetation structure over the period 30 to >40 years suggests that fire frequencies in this range may be appropriate to maximise structural complexity.

Implications for malleefowl

The malleefowl is subject to several threats across its range, including predation by foxes, destruction of habitat, grazing by introduced herbivores and inappropriate fire regimes. Widespread and too frequent fire has been suggested as responsible for the local disappearance of malleefowl from parts of south-west WA (Milligan 1903; Carter 1923). It is unlikely that too frequent fire represents a current threat to malleefowl within the WA wheatbelt as intervals for small and large remnants (339 and 67 years respectively) exceed the 60-year minimum suggested by Benshemesh (1992) as appropriate for malleefowl. These intervals are also likely to be underestimates of interval length for any particular location as they do not account for the patchiness of fires within a sample. It is more likely that threats other than fire (e.g. predation, habitat loss and fragmentation) are more significant in this region (Benshemesh 2007; Parsons *et al*. 2008).

Conversely, continuous vegetation adjacent to the wheatbelt showed an average fire interval of 40 years, which is less than the recommended interval for malleefowl. Further, fires were very large. Extensive, homogeneous and too-frequent fires are known to have deleterious and long-lasting effects on malleefowl (Benshemesh 1992), and similar fire regimes are operating and threatening malleefowl in large remnants and continuously vegetated landscapes in eastern Australia (Benshemesh 1990). Management aimed at retaining more long-unburnt habitat may be appropriate, although guidance as to how this might be achieved in practice is currently lacking (Clarke 2008).

The differences in habitat response to fire between mallee-shrub and *Acacia* shrubland (malleefowl rarely use mallee-heath) suggest that they are most suitable for malleefowl over different periods of the fire cycle. An important element of malleefowl habitat is a varied understorey, which can provide food at different times of the year including during drought (Harlen and Priddel 1996), and abundant litter cover for mound construction. Mallee-shrub retains substantial litter cover and understorey structure 45 years post-fire and beyond, suggesting that this habitat is likely to remain suitable for malleefowl for long periods in the absence of fire. Conversely, understorey and litter cover peak ~25 to 30 years post-fire in *Acacia* shrublands, then decline. Therefore, it is plausible that as *Acacia* shrublands age, they may become less suitable for malleefowl.

A *lack* of fire may now consequently represent a long-term threat to malleefowl in small *Acacia* shrubland remnants. The active reintroduction of fire may be an appropriate management response, although managing the interaction of fire and other processes that degrade native vegetation in small remnants (e.g. weed invasions, salinity; Hobbs and Yates 2003) presents a considerable challenge. Quantitative research examining the effect of senescing vegetation on malleefowl abundance and density would clarify whether an absence of fire poses a genuine threat to the species.

We found that the three habitats developed structural attributes of importance to malleefowl over a time period considerably shorter (i.e. between 25 and 45 years) than the recommended fire interval for the species of 60 years (a cautious overestimate based on breeding densities; Benshemesh 1992). This may be due to higher productivity of our study areas compared with those of Benshemesh (1992), as mean annual rainfall was over 90 mm greater in our study area (Bureau of Meteorology, see http://www.bom.gov.au/climate/data/, accessed March 2011). Further, congruence of peak habitat suitability and population density may be unlikely owing to density being influenced by other factors (e.g. predation) and the malleefowl's reproductive and behavioural ecology. Therefore, for malleefowl conservation, we suggest that a conservative approach to fire management that considers both direct fire effects on the species and its habitat, and other environmental stressors, is necessary.

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